DECAY AND FOSSILIZATION OF NON-MINERALIZED TISSUE IN COLEOID CEPHALOPODS

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ABSTRACT. Decay experiments were carried out on three Recent species of coleoid cephalopods (the squids *Alloteuthis subulata* and *Loligo forbesi*, and the sepiolid *Sepiola atlantica*) over a period of 1 day to 50 weeks. The morphological sequence of degradation and the fate of the more decay resistant organs (beaks, radula, suckers, gladius, statoliths, eye lenses) were recorded. Crystalline magnesium phosphate precipitated, but tissue ultrastructure was not preserved. Sex and stage of maturity may influence rate of degradation. Differences in buoyancy mechanism, physiological changes during reproduction, and post-mortem decay processes affect the highly variable preservation potential of modern coleoids.

Of the six genera (*Belemnotheutis*, *Mastigophora*, *Loligosepia*, *Geopeltis*, *Plesioteuthis* and *Trachyteuthis*) of exceptionally preserved Jurassic fossil coleoids examined for evidence of ultrastructural preservation, *Mastigophora* exhibits a continuous series of tissues from the outer tunic, through the mantle and gladius, to the muscular sheath of the digestive gland. In *Belemnotheutis* and *Mastigophora* the radial and circular muscle, the outer collagenous tunic and the supporting meshwork of intramuscular fibres are all preserved. Longitudinal fibres are evident in the arms and in the mantle of some specimens. The texture of the calcium phosphate replacing the soft-tissue varies even within a specimen. Muscles may be represented by the fibres, or only the sarcolemma. The microspheres of calcium phosphate are 1–2 μm in diameter in the former (perhaps representing the microbes themselves), but only 0·1 μm in the latter (where precipitation is induced by microbial processes). Microspheres in the tunic are 0·5–0·25 μm in diameter. Muscle, tunic, intramuscular fibres and ink are preserved in calcium phosphate. Gladius material is finely banded, with varying proportions of diagenetic calcium phosphate and calcium carbonate in each of the layers in *Geopeltis* from Charmouth. The mantle morphology found in *Mastigophora* and *Belemnotheutis* corresponds with that found in living coleoid cephalopods and indicates that this structure had evolved by the Early Jurassic. This calls into question the systematic position of *Belemnotheutis* as a member of the Belemnitida. It is clear that phosphatization of ultrastructural detail is not confined to a small number of unusual localities. There is considerable potential for histological investigations of the soft-tissues of a range of extinct organisms.

THE Coleoidea, typified by the extant squids, cuttlefish and octopus, rank alongside the Nautiloidea and Ammonoidea as the third major subclass of cephalopods. Whilst the nautiloids and ammonoids have a heavy external shell, most coleoids, with the exception of the living families Sepiidae and Spirulidae and the extinct order Belemnitida, have negligible mineralized tissue and are essentially soft-bodied. Nevertheless the soft tissues of coleoid cephalopods are preserved at a number of Jurassic localities (Table 1), e.g. Holzmaden (Toarcian), Germany; Christian Malford (Callovian), England (Donovan 1983; Allison 1988; Page 1991; Donovan and Crane 1992); Voulte-sur-Rhône (Callovian), France (Fischer and Riou 1982*a*, *b*); Solnhofen (Tithonian), Germany (Bandel and Leich 1986; Mehl 1990), as well as in the Cretaceous (Albian) of NW Queensland (Wade 1993), the Carboniferous Mazon Creek biota of Illinois (Allison 1987) and possibly the Devonian (Emsian) Hunsrückschiefer of Germany (Stürmer 1985). Whilst the morphology of a number of coleoids that preserve traces of the soft parts has recently been described in detail from these localities, the mineralization of the soft-tissues has only been subjected to preliminary investigation (Allison 1988; Mehl 1990). The aim of this study is to identify the tissue types preserved in coleoids, to determine the degree of morphological detail preserved, and to interpret this in the light of controlled decay

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TABLE 1. Types of soft tissues reported in fossil coleoids. —, feature is not preserved; ?, feature may be preserved; n/a, feature would not normally occur in the coleoids represented in this fauna. Sources of information: Fischer and Riou 1982*a*; Donovan 1983; Bandel and Leich 1986; Allison 1987, 1988; Mehl 1990; Donovan and Crane 1992.

	Tissue/organ						
Locality	Mantle	Arms	Tentacles	Jaws	Gills	Ink sac	Gladius
Solnhofen	Present	Present	?	Present	Present	Present	Present
Voulte-sur-Rhône	Present	Present	Present	Present	—	Present	Present
Christian Malford	Present	Present	Present	—	—	Present	Present
Holzmaden	Present	—	—	—	—	Present	Present
Lias	—	—	—	—	—	Present	Present
Mazon Creek	—	Present	n/a	Present	—	?	Present

experiments on recent cephalopods. Only when the decay process is understood can fossil tissue be reliably interpreted by comparison with living analogues. This has allowed the evolution of mantle ultrastructure in coleoids to be analyzed. Controls on mineralization were investigated in other experiments using smaller animals (polychaetes and shrimps) which are more easily obtained and processed in the sample sizes required (Briggs and Kear 1993*a*, 1993*b*, 1994; Briggs *et al.* 1993).

COLEOID HISTOLOGY AND ULTRASTRUCTURE

Living coleoids have a range of structural tissues of differing composition and resistance to decay (Table 2). The chitin of the buccal mass and digestive system is interconnected and may form a continuous sheet (Kear 1990), starting at the inner surfaces of the lips and encompassing the beaks, hyaline shield of the radula, buccal palp surface and teeth, and oesophageal and stomach lining. Lip chitin has only been reported in adult *Mesonychoteuthis* (Kear 1990). The radular teeth, which originate separately to the hyaline shield (Nixon 1968) and differ in composition, may not be part of this continuum.

Secretion and tanning of the chitin in beaks is carried out by epithelial cells known as beccublasts (Dilly and Nixon 1976), which act as holdfasts for the mandibular muscles (Dilly and Nixon 1976), as well as performing a secretory function. Similar 'chitinoblast' cells are found in association with the radula and hyaline shield (Nixon 1968), buccal palps, oesophagus and possibly the papillary shield (Kear 1990).

The muscular mantle of coleoids is used for both propulsion and respiration. The mantle of the Decapoda (= Decabrachia) (Text-fig. 1) is composed of a thick layer of circular muscle partitioned into bands by thin sheets of radial muscle (Ward and Wainright 1972; Bone *et al.* 1981). Longitudinal muscles have only been observed in *Sepia officinalis* (Bone *et al.* 1981). Layers of parallel collagen fibres (Text-fig.1) encase the mantle muscle, running around the mantle (the inner and outer tunics) in alternate left and right-handed helixes (Ward and Wainright 1972). In addition, there is a network of intramuscular connective tissue within the mantle (Ward and Wainright 1972; Bone *et al.* 1981). This tissue consists of fibres composed of collagen (Bone *et al.* 1981; Gosline and Shadwick 1983) and possibly elastin (Bone *et al.* 1981) and forms a mesh throughout the muscle (Text-fig. 1). The tunics and mesh resist length changes in the mantle during contraction (Ward and Wainright 1972).

Decapod coleoids (Teuthida, Sepiida and Sepiolida) have four pairs of arms and one pair of tentacles; the latter are a specialist prey capture mechanism with suckers present only on the

TABLE 2. Location and composition of the main structural tissues (where present) in living coleoid cephalopods.

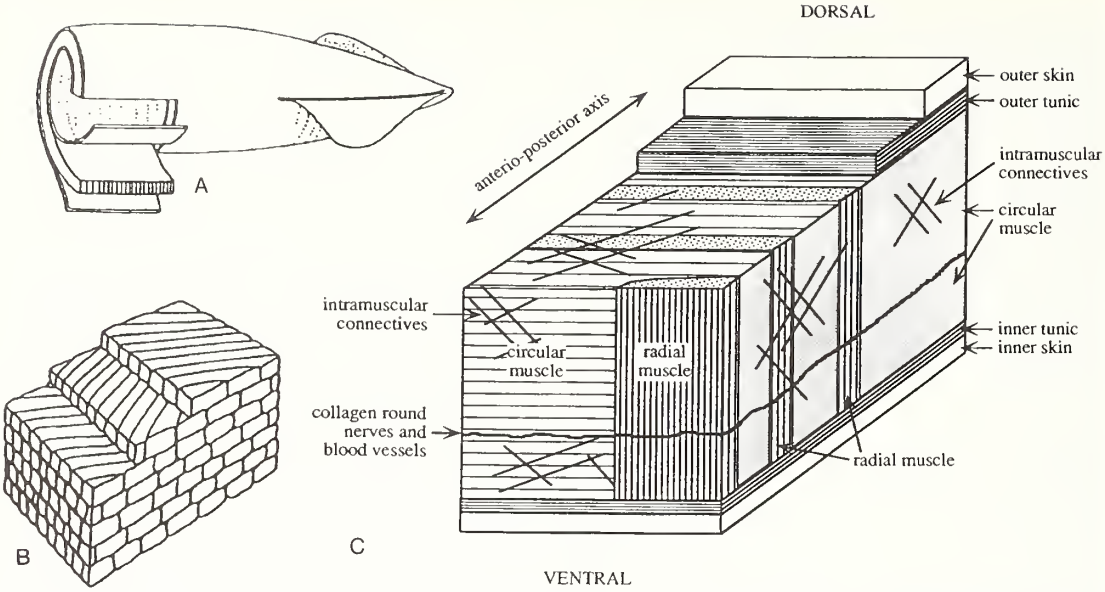
Tissue/organ	Composition	Author
Suckers and/or hooks	β chitin	Hunt and Nixon 1981
Lip lining	Chitin (?type)	Kear 1990
Beaks	α chitin	Hunt and Nixon 1981
Radula	α chitin	Hunt and Nixon 1981
Hyaline shield	chitin (?type)	
Buccal palp teeth	α chitin	Hunt and Nixon 1981
Oesophagus lining	Chitin (?type)	Kear 1990
Stomach lining	γ chitin	Rudall and Kenchington 1973
	α chitin	Rudall and Kenchington 1973; Hunt and Nixon 1981
Brain and nuchal cartilage	Collagen	Nesis 1987
Statoliths	Aragonite	
Eye lenses	Crystallin	
Mantle locking cartilage	Collagen	Nesis 1987
Gladius	β chitin	Rudall and Kenchington 1973; Hunt and Nixon 1981
Internal shell	Calcite and chitin	
Skin tubercles	Collagen	Nesis 1987
Tunics of mantle muscle	Collagen	Ward and Wainright 1972; Bone *et al.* 1981; Gosline and Shadwick 1983
Intramuscular mesh	Collagen	Bone *et al.* 1981; Gosline and Shadwick 1983
	Elastin	Bone *et al.* 1981

terminal portion. In resting position the tentacles are retracted within the cone of the arms, or into special pouches (cuttlefish). Certain species of squid only possess tentacles as juveniles. The musculature of both arms and tentacles is more complex than that of the mantle, consisting of longitudinal, transverse, circular, oblique and helical muscle (Kier 1982, 1988), the last in the tentacles only.

The muscular tissues may undergo substantial morphological changes as a coleoid matures. A number of species resorb their own tissues – particularly mantle, tentacles and arms – to provide energy and resources for gonad growth. This is seen at its most extreme in the squid *Moroteuthis ingens*, in which immature females have thick (up to 10 mm), muscular mantle walls, but mature individuals have a thin, gelatinous mantle (Jackson and Mladenov 1994). Histological examination reveals that the tissue breakdown is due to a loss of muscle, leaving only the intramuscular collagen fibres intact. In spent (i.e. post-spawning) individuals even the collagen breaks down. None of these changes is as extreme in males of the same species (Jackson and Mladenov 1994). In contrast, species which need to retain swimming ability for long migrations to spawning grounds show no loss of mantle integrity with maturation (e.g. *Illex argentinus*; Clarke *et al.* 1994).

There are phylogenetic contrasts as well. In neutrally buoyant families, such as the Architeuthidae and Histioteuthidae, active swimming ability is not needed, and only the fins and tentacles are strongly muscular. Similarly, in some of the oceanic octopods (e.g. Cirroteuthidae, Vitreledonellidae), the 'muscular' layer of the mantle is a watery cellular matrix with sparse collagenous and muscle fibres even in juveniles (Nesis 1987). The preservation potential of coleoids therefore varies widely.

Underlying the mantle is the gladius (pen), a chitinous sheet for support and muscle attachment. Muscle and connective tissue surround the digestive gland and other internal organs.



TEXT-FIG. 1. Diagrammatic representation of coleoid mantle and tunic morphology. A, squid body, showing the position of outer tunic, mantle muscle and inner tunic; B, the layered structure of the tunic; C, a section through the skin and upper mantle, showing muscle morphology in relation to the anterio-posterior axis of the animal; radial and circular muscle and intramuscular connectives are marked; patterning on the muscle indicates fibre orientation. A–B re-drawn, with permission, from Ward and Wainright (1972).

MATERIALS AND METHODS

Recent coleoid cephalopod material was obtained from the Plymouth Marine Laboratory, UK. The squids *Alloteuthis subulata* and *Loligo forbesi* (Teuthida: Loliginidae) and the cuttlefish *Sepiola atlantica* (Sepiolida: Sepiolidae) were trawled off Plymouth. The animals used for experiments were those which were brought up dead or dying in the nets, or died overnight in the stock tanks. Only the heads of *Loligo* ($n = 16$: dorsal mantle length 135–295 mm; body weight 111·7–587·9 g) were utilized in experiments. Whole *Alloteuthis* ($n = 16$: dorsal mantle length 60–85 mm) and *Sepiola* ($n = 4$: dorsal mantle length 15–20 mm) were utilized.

Specimens were placed in 250 ml Kilner jars with 150 ml (*Alloteuthis*, *Sepiola*) or 200 ml (*Loligo*) of seawater from the Plymouth Marine Laboratory's research circulation (salinity 33·1 ppt; pH $7{\cdot}63 \pm 0{\cdot}06$) and transferred to an incubator at 20 °C within 4 hours. These experiments correspond to the 'slow diffusion' type (1b) of Briggs and Kear (1993*a*, 1994).

Specimens were inspected/sampled after 1, 2, 3, 4, 7 and 10 days and after 2, 3, 4, 6, 8, 10, 15, 20, 25, 30 and 50 weeks. Morphological changes were recorded without opening the jars or disturbing the carcass. Sampling for analysis involved decanting off the seawater and filtering or sieving the remains. More decay resistant organs (beaks, radula, statoliths, eye lenses, gladius, suckers) were removed and fixed in alcohol. Material was fixed for SEM using the glutaraldehyde-HMDS method (Nation 1983). The remains of the carcass were oven-dried at 105 °C to constant weight. The colour and pH of the seawater within the experimental vessel were noted. Crystalline material was removed from the carcass for analysis with the electron microprobe.

Fossil coleoids which commonly preserve muscle fibres are likely to preserve other soft tissues. Exceptionally preserved material held in the collections of the Natural History Museum (NHM) and Bristol City Museum (BRSMG) was therefore examined (see Appendix). The investigation

TABLE 3. Decay stages in *Alloteuthis* and *Sepiola*.

After 1 day: Post-mortem
The carcass is firm. The outer layer of mantle skin shows signs of disintegration while the chromatophores of the inner layer contract, giving the animal a pale appearance. The skin shrinks away from the mantle in places, revealing the muscle underneath, which turns opaque white. The ink behaves as a liquid. Some eggs escape down the funnel of a mature female *Sepiola*.

After 2 days: Osmotic effects
The muscle (arms, funnel, mantle, fins) becomes soft. The arms and mantle may be swollen. The swollen egg mass of mature *Sepiola* displaces and tears the mantle.

After 3 days: Shrinkage
The arms and eyes, and some of the outer layer of skin, begin to detach from the carcass. Pigment granules are scattered in the water. The muscles disintegrate if disturbed. The body and arms have shrunk, and contraction of the mantle reveals the edge of the ink sac, anus and spermatophoric duct. The gladius of *Alloteuthis* may protrude from the front of the mantle, but is structurally indistinguishable from fresh material (Text-fig. 3D). The gills may be swollen. The muscle of the head has shrunk, making the eyes appear disproportionately large. A bulge in the arm cone may represent the folded tentacles swollen in their "pouch". The chitinous arm suckers may remain in place (*Sepiola*) (Text-fig. 3F) or be mainly detached due to decay of the attachment muscles (*Alloteuthis*). The ink solidifies.

After 1 week: Disintegration begins
The carcass shrinks further and collapses unless the shape of the mantle is maintained by reproductive material inside (in female *Alloteuthis*). Surviving pigment is very dark. The fins may detach, and the head drifts away from the mantle. The beaks and radula remain in the buccal mass, although the edges of the beaks may have disintegrated. The gladius becomes brittle. Few sucker rings are still attached. Retinal pigment may stain the eye lenses, beaks, and pen. The outer membranes of the ink sac disintegrate, but the ink remains a unit. The digestive gland may still be evident. The spermatophores of *Sepiola* survive as bunches of transparent tubes, some still containing sperm. The gills of *Alloteuthis* remain evident and possible nidamental glands are visible in females. In places a layer of white crumbly mineralized material is present beneath the pigment layer, but above the mantle muscle. Although the quantity was inadequate for analysis, the crystal form and occurrence are similar to magnesium phosphate that sometimes precipitated in decay experiments on the shrimp *Palaemon* (Briggs and Kear 1994).

After 2 weeks
The carcass has shrunk to several amorphous masses. The outline of the arms and the associated eye lenses remains evident. The ink and remains of mantle may survive as one unit (*Sepiola*) or the gonad alone is intact and three-dimensional (*Alloteuthis*). Other internal organs have completely decayed or are unrecognizable. Eggs are scattered. The beccublast cells appear white and fibrous and retain their original structure in *Alloteuthis*. A thin membrane peels away from the inner surface of the gladius (Text-fig. 3E). A white coating of mineralized material (probably $MgPO_4$) may be present on the upper surface of gonad and some muscle, as well as on the bottom of the jar. It occurs either as a thin structureless crust or as scattered crystal laths and needles.

After 8–10 weeks
The head and mantle disintegrate further, and muscle peels away from the pen in places. The arms may be recognizable. The eyes are visible as dark purple areas surrounding the lenses. The gonad remains three-dimensional only in *Alloteuthis*.

focused on *Belemnotheutis antiquus* (Belemnitida: Belemnotheutidae) and *Mastigophora brevipinnis* (Teuthida: Mastigophoridae) from Christian Malford, Oxfordshire (Jurassic, Callovian), but material of *Plesioteuthis prisca* (Teuthida: Plesioteuthididae) and *Trachyteuthis hastiformis* (Teuthida: Trachyteuthidae) from Solnhofen (Jurassic, Tithonian); *Loligosepia* (= *Geoteuthis*) sp. (Teuthida: Loligosepiidae) from Gloucestershire and Somerset (Jurassic, Upper Lias); and

TABLE 4. Decay stages in *Loligo*.

After 1 week
The head begins to swell. The outer muscle is stained pink. The sucker rings are fragile and detach easily (Text-fig. 3G). The eyes are represented by dark patches and may have separated from the carcass. The lenses remain intact and the brain cartilage is hard. The buccal muscles shrink and lose their shape when disturbed. The beaks pull out with no resistance; lip muscle tissue may remain attached to the lower beak.

After 2 weeks
Gas bubbles are present under the skin. The sucker rings, statoliths and eye lenses are stained pink by retinal pigment. The eyes and tentacles fall off and most of the sucker rings detach. The buccal muscle tissue disintegrates. The brain cartilage becomes soft and spongy and no neural tissue remains.

After 3–4 weeks
The head may float due to the presence of additional gas bubbles. The manus of the tentacles, the eyes and much of the muscle disintegrates. The untanned areas of the beaks are now stained. The anterior of the radula disintegrates. Dark purple-pink crystals of $MgPO_4$ form in the skin of the arms and around the shrinking brain cartilage.

After 6 weeks
The head disintegrates to an amorphous semi-liquid. The beaks disarticulate; some semi-liquid muscle adheres inside the hood area. Only the eyes, brain cartilage and arms are recognizable. Nearly all the sucker rings detach.

After 10 weeks
Only the arms, tentacles, and a few sucker rings are recognizable, but they disintegrate if disturbed. Many doughnut- and spiral-shaped crystals of magnesium phosphate (Table 5) occur loose and on the arms; they form on the sucker rings which may be embedded within them (Text-fig. 3H–I). Their purple colour is derived mainly from the retina, and to a lesser extent from the chromatophores.

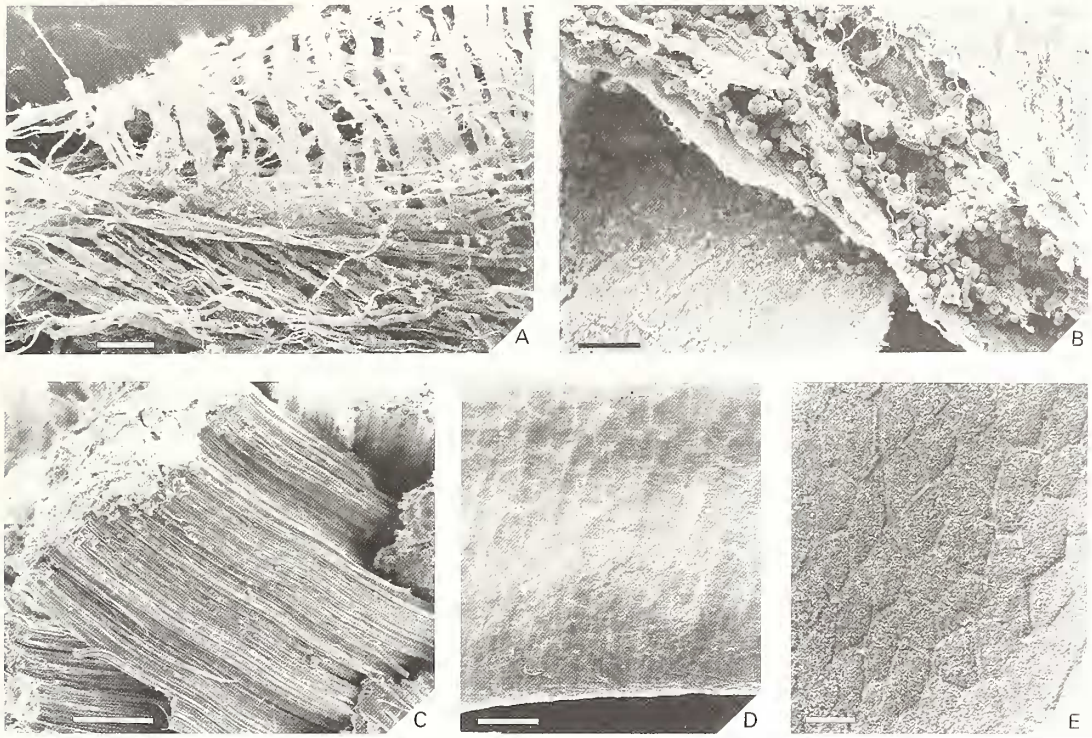
After 15–30 weeks
A crumbly, largely amorphous mass containing crystals, either individual or clusters of needles up to 3 mm long, covers the bottom of the experimental vessel. Parts of the arms and tentacles may be recognizable. The brain cartilage has largely disappeared. The edges of the beaks decay. The radula disintegrates if disturbed.

After 50 weeks
The beaks and part of the radula are evident, together with crystals, in a mass of semi-liquid tissue. There is no trace of the suckers.

Geopeltis simplex (Teuthida: Geopeltidae) from Boll, Württemberg, Germany (Jurassic, Upper Lias) was also examined.

Small pieces of phosphatized mantle were removed from specimens of the Christian Malford taxa *Belemnotheutis antiquus* (specimens NHM C.46898 and NHM C.2456) and *Mastigophora brevipinnis* (NHM 31362, NHM 46964 and NHM 62231) for investigation by scanning electron microscopy. Where possible, the orientation of the fragments relative to the anterio-posterior axis of the specimens was noted. Muscle fragments from *Mastigophora brevipinnis* (NHM 31362) were analyzed by electron microprobe.

A specimen of *Geopeltis* sp. (University of Bristol, Geology Department, BRSUG 25602) from Black Ven, Charmouth, Dorset (Jurassic, Lower Lias) was sectioned and polished for analysis by light microscopy, SEM and electron microprobe.



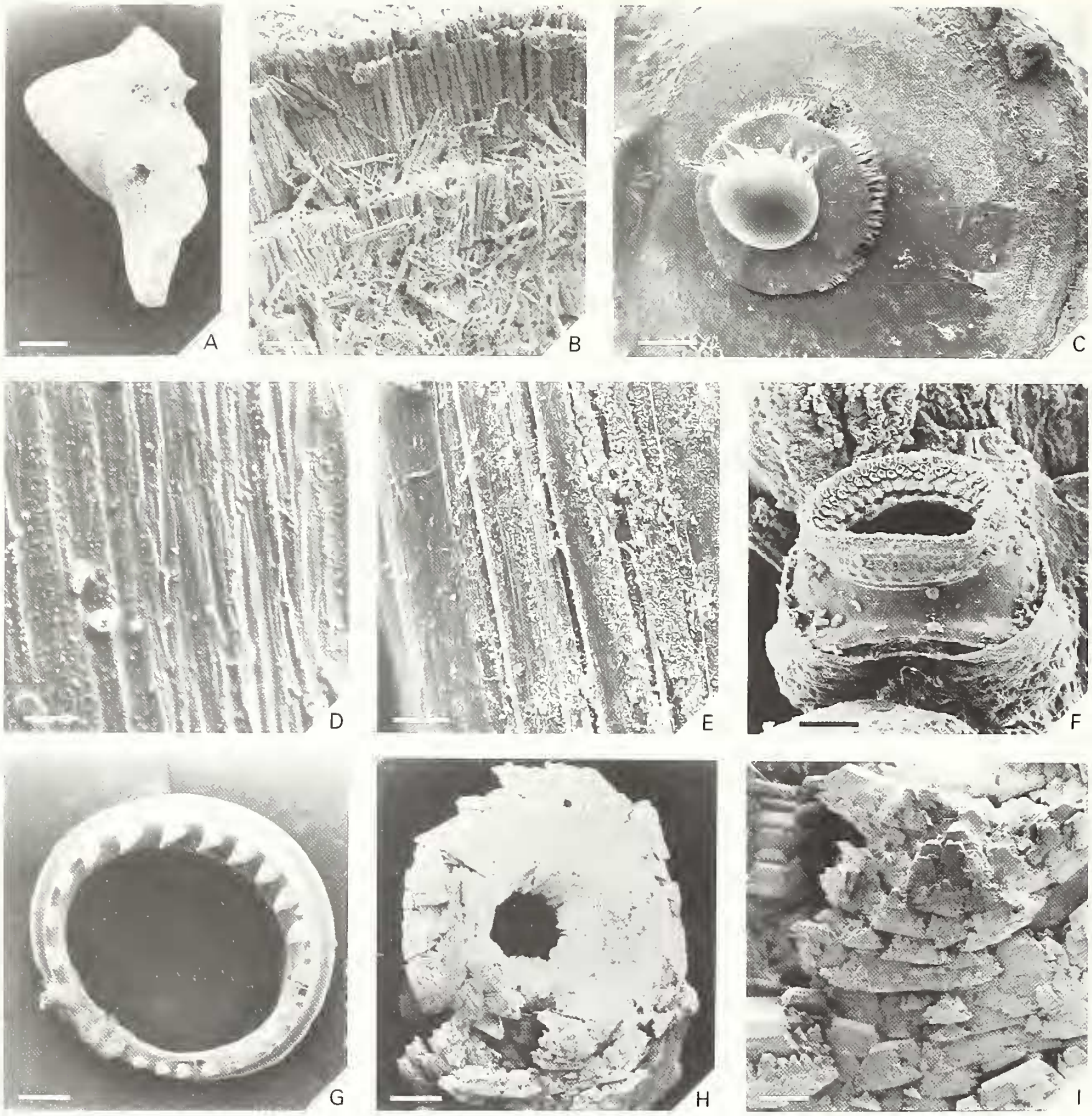
TEXT-FIG. 2. SEM micrographs of soft-tissue decay in slow diffusion conditions. A, *Sepiola atlantica* mantle at 1·5 days, fixed in HMDS for SEM examination. The muscle has largely decayed away, but collagenous tissues (tunics, intramuscular connectives) remain intact. The fibres in the upper portion of the picture have 'unravelled' during specimen handling. Scale bar represents 20 μm. B, same specimen as A showing the cut edge of the mantle. Intramuscular connectives are visible, running between the inner and outer tunic layers. The collagen is covered with bacteria of 2–4·5 μm in diameter; compare with phosphate spheres in fossil material in Text-fig. 4. Scale bar represents 20 μm. C, *Alloteuthis subulata* after 4 weeks, oven dried. Fibrillar phase beccublast cells still insert on the upper beak. The fibrils still cluster into hexagonal clumps, which probably represents the original position of the cells. Scale bar represents 40 μm. D, the rear edge of the upper beak crest in *Alloteuthis subulata* after 3 days. The polygonal imprints left by beccublast cells are evident. The chitin of the beak is undecayed at this stage. Scale bar represents 20 μm. E, *Loligo forbesi* sucker surface after 3 weeks. The attachment muscles have decayed away, leaving polygonal imprints of chitinoblast cells similar to the beccublasts in D. Scale bar represents 10 μm.

RECENT COLEOIDS

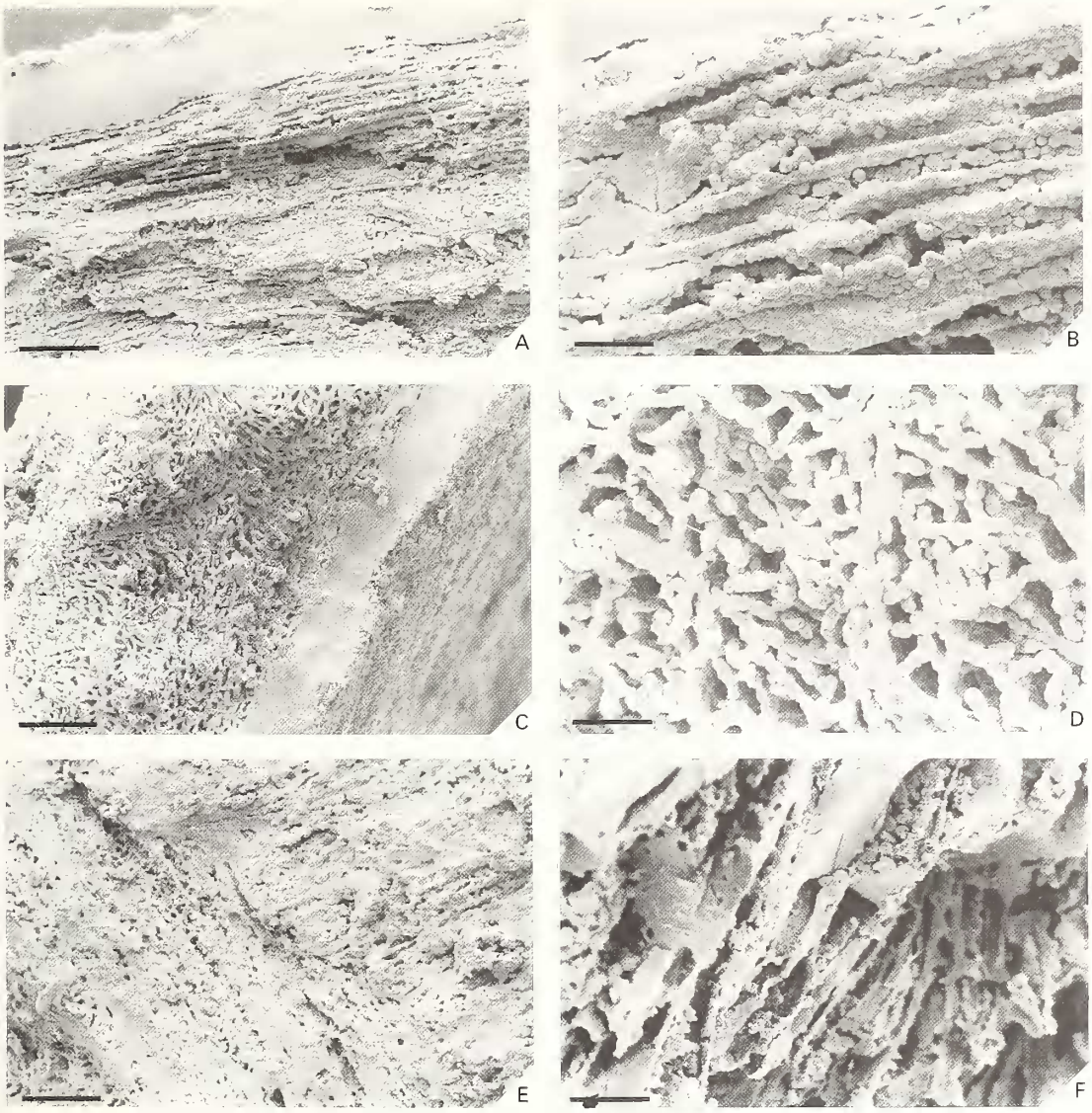
Death and decay stages

In both experimental and aquarium conditions dead and dying *Alloteuthis*, *Sepiola* and *Loligo* lie on the bottom of the tank. They are ignored by their companions. In contrast, dying *Sepia* float at or near the surface in both aquarium and natural conditions, and are frequently attacked by conspecifics as well as being an easy target for epipelagic and aerial scavengers. Thus, the mode of dying affects the preservation potential of a given taxon.

The tentacles are not normally extended at death and should therefore be concealed in undisturbed carcasses. Any tilting of the carcass head downwards during handling, however, can cause the tentacles to slide from their 'pouch', and they also hang down in this way in anaesthetized and dying *Sepia*.



TEXT-FIG. 3. Decay of structural tissues in recent coleoids under conditions of slow diffusion. A, statolith from an undecayed *Loligo forbesi*. Scale bar represents 400 μm. B, surface of *Loligo* statolith after 4 weeks. The statolith is exfoliating and individual aragonite rhombs are becoming loose. Scale bar represents 10 μm. C, eye lens from *Alloteuthis subulata* after 3 days. The lens has been broken along the natural fracture plane to show the internal structure. Scale bar represents 200 μm. D, ventral side of *Alloteuthis* gladius after 3 days. A membrane covers the surface, obscuring detail of the structure beneath. Scale bar represents 20 μm. E, ventral view of *Alloteuthis* gladius after 1 week. The thin membrane has peeled away and the chitin beneath is splitting along natural growth lines. Bacteria are visible on the gladius surface. Scale bar represents 20 μm. F, sucker *in situ* on the arm of *Sepiola atlantica* after 1·5 days. The attachment muscles still hold the sucker ring in place. Scale bar represents 40 μm. G, a detached sucker ring from *Loligo* after 1 week. No muscle tissue remains adhering to the chitin. Scale bar represents 400 μm. H, *Loligo* sucker removed from an arm after 10 weeks. The sucker has been overgrown by magnesium phosphate crystals in a spiral pattern. No organic component remains visible. Scale bar represents 400 μm. I, close-up of H to show crystal structure. Scale bar represents 100 μm. Specimens illustrated in C to F were dehydrated in HMDS prior to SEM examination.



TEXT-FIG. 4. SEM of muscle tissue from fossil coleoids. A, transverse section of *Belemnotheutis antiquus* (NHM C.2456) mantle muscle. Fibrous structure is clearly visible. The massive band at the top of the picture is a layer of varnish. Scale bar represents 40 μm. B, close-up of A showing the 1–2 μm microspheres of calcium phosphate which make up the muscle fibrils. Scale bar represents 10 μm. C, longitudinal section of the same specimen with the muscle fibres viewed end on. The massive band on the right is a layer of varnish. Scale bar represents 40 μm. D, close-up of C showing microspheres 1–2 μm in diameter. Scale bar represents 10 μm. E, *Belemnotheutis* (NHM C.46898) mantle with two sets of muscle fibres meeting at 90°. Scale bar represents 40 μm. F, *Mastigophora brevipinnis* (NHM 62231) muscle tissue from the digestive gland sheath. The collagenous sarcolemma is preserved but the fibrils themselves have decayed away. Scale bar represents 10 μm.

The flesh of *Alloteuthis*, *Sepiola* and *Loligo* starts to become opaque *before* they stop respiring, indicating that histochemical changes in the mantle can occur prior to actual death. The flesh of *Sepia* is opaque in life.

TABLE 5. Composition of mineral phases in fossil coleoids and decaying *Loligo*. Oxide weights based on electron microprobe analyses (total given as weight per cent. of sample mineralized). Ratio of calcium phosphate to $CaCO_3$ based on the assumption that all P_2O_5 is incorporated into ideal OH-apatite [$Ca_5(PO_4)_3OH$]. The $CaO:P_2O_5$ ratio is 1:1·32 (based on molecular weights, ignoring H and excess O). The remaining CaO is assumed to form $CaCO_3$.

Specimen	% by wt	Na_2O	MgO	SiO_2	Al_2O_3	P_2O_5	SO_3	FO	CaO	CaO in phosphate	Phos:carb (%)
Geopeltis											
Pen layer 1	60·8	0·2	0·6	0·04	—	1·9	0·1	1·0	56·0	2·5	4·5:95·5
Pen layer 2	88·1	2·6	0·3	—	0·05	32·2	1·2	3·2	48·4	42·5	87·8:12·2
Pen layer 3	65·1	0·5	0·7	—	—	11·7	0·4	1·5	49·5	15·4	31·1:68·9
Pen layer 4	88·0	1·3	0·3	—	0·02	31·8	1·0	4·0	49·4	42·0	85·0:15·0
Pen layer 5	70·8	0·7	0·6	—	0·01	16·9	0·7	1·7	49·3	22·3	45·2:54·8
Pen layer 6	95·1	0·8	0·4	—	0·02	33·9	1·4	4·8	53·5	44·7	83·6:16·4
Ink sac	83·2	1·5	0·3	—	0·01	30·4	1·7	3·2	45·8	40·1	87·6:12·4
Rock	56·5	0·3	0·8	2·1	0·83	2·2	0·5	0·2	48·9	2·9	5·9:94·1
Mastigophora											
Radial	86·1	0·9	0·3	—	—	32·5	0·5	1·9	49·6	42·9	86·5:13·5
Circular	85·6	1·0	0·3	—	0·02	32·4	0·4	1·6	49·5	42·8	86·5:13·5
Rock	75·9	0·4	1·7	34·8	17·54	0·8	2·9	—	10·4	1·1	10·6:89·4
Loligo (4w)											
Sucker crystal	58·2	0·1	20·6	—	0·02	37·4	0·1	0·1	0·1	0·1	—

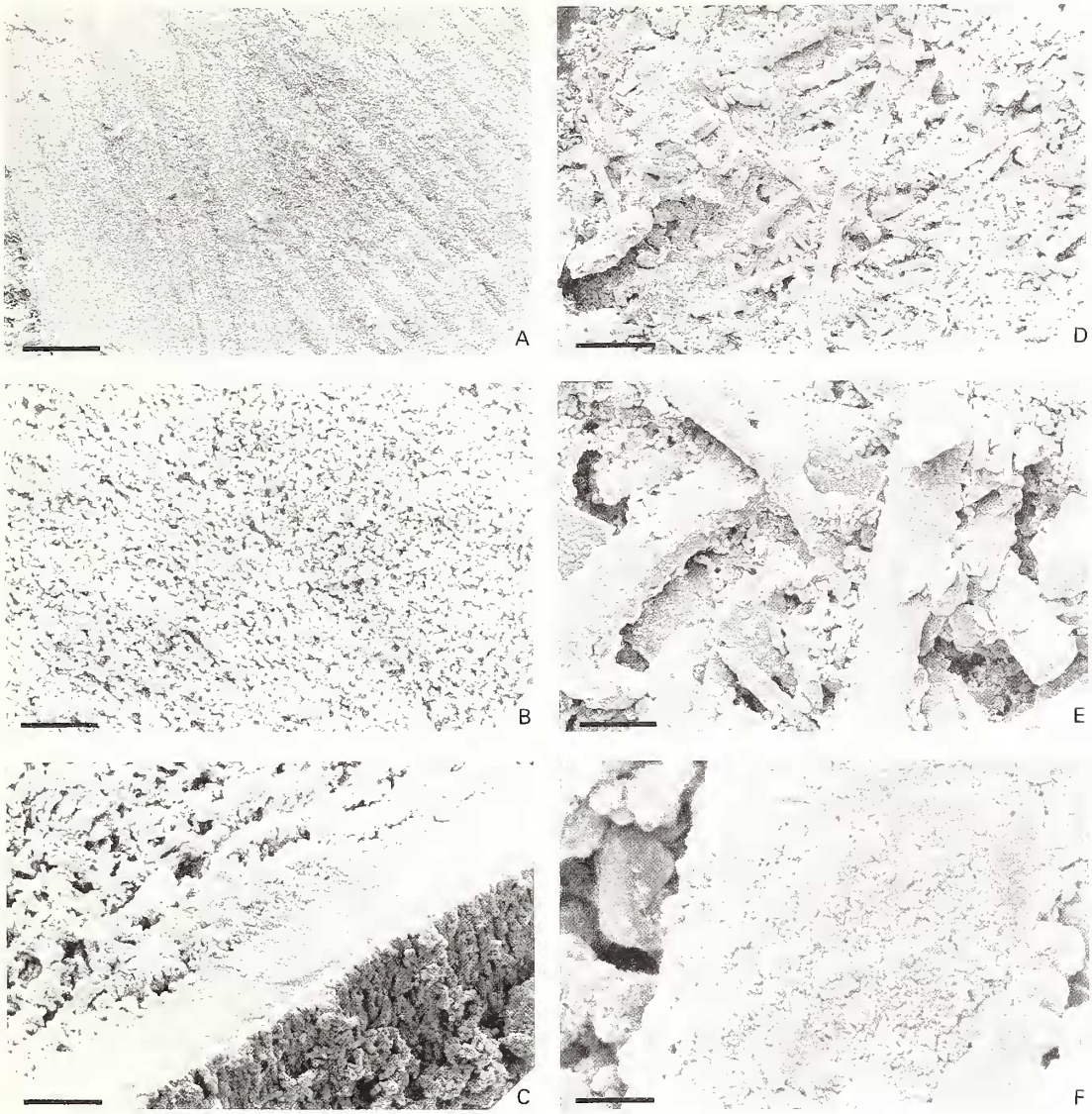
TABLE 6. Ultrastructural features preserved in fossil coleoids examined by light and electron microscopy.

Species	Outer tunic	Inner tunic	Radial muscle	Circular muscle	Intramuscular mesh	Gladius structure
Belemnotheutis	Yes	?	Yes	Yes	Yes	Yes
Geopeltis	?	—	Yes	Yes	—	Yes
Loligosepia	Yes	—	Yes	Yes	—	—
Mastigophora	Yes	Yes	Yes	Yes	Yes	?
Plesioteuthis	Yes	—	Yes	Yes	—	Yes
Trachyteuthis	—	—	?	?	—	Yes

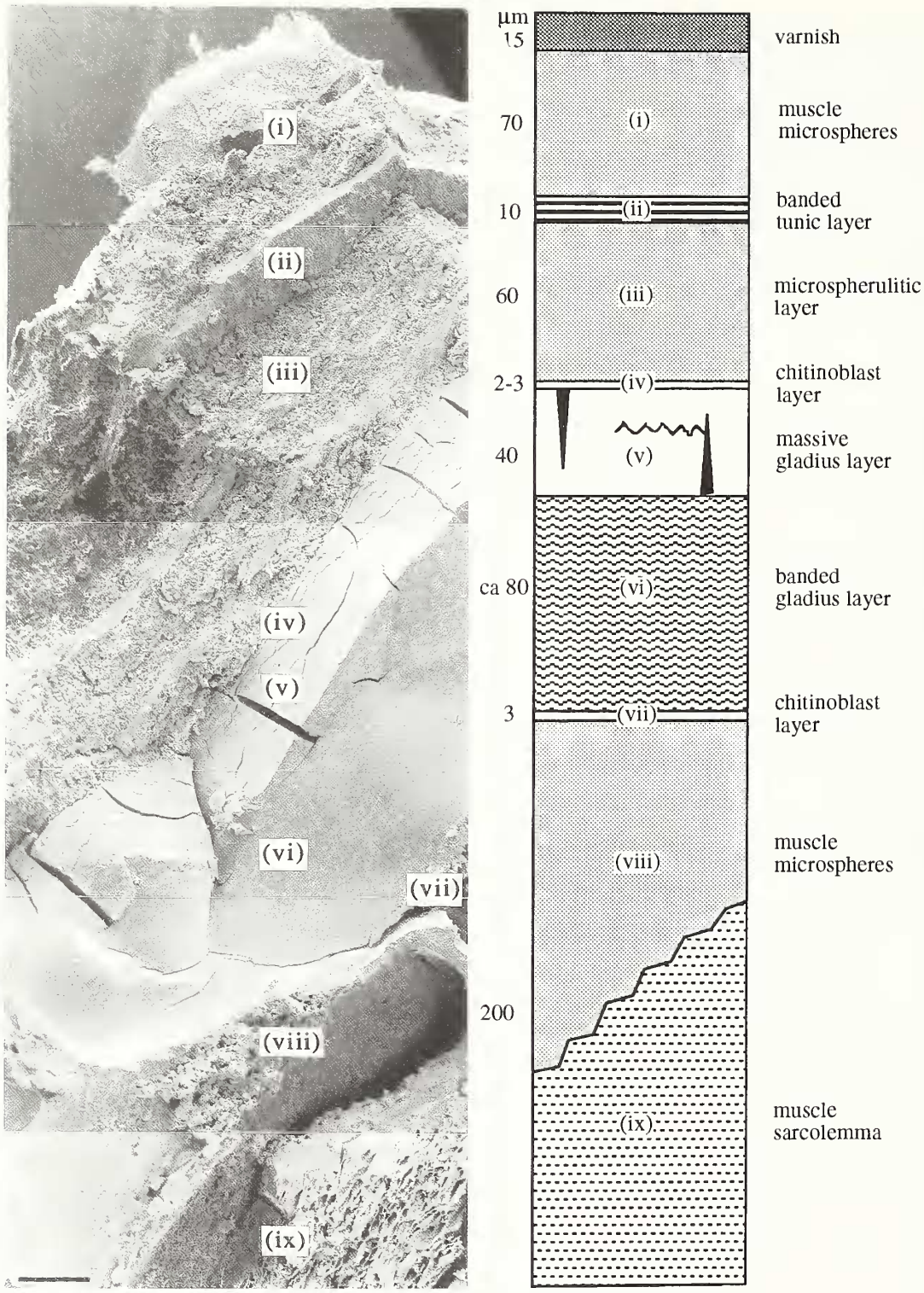
Degradation is very similar in carcasses of *Alloteuthis* and *Sepiola* (Table 3). Only the head and arm crown portion of *Loligo* were utilized in decay experiments, and studies concentrated on the fate of the structural materials (chitin, collagen, crystalline protein, aragonite) and on the precipitation of minerals in and around the carcass (Table 4).

Ultrastructural decay and preservation

Muscular disintegration is rapid in all three coleoid species and ultrastructural detail is lost in as little as 1·5 days. The collagenous component of the muscle (tunic layers and intramuscular connectives) survives longer than the fibrils themselves (Text-figs 2A, B), and is probably responsible



TEXT-FIG. 5. SEM of collagenous connective tissues from fossil coleoids. A, two outer tunic layers from the ventral surface of *Belemnotheutis antiquus* (NHM C.2456) (see Text-fig. 1B). The fibres cross at an angle of 30–32°. The axis of the body bisects this angle in living species. Scale bar represents 100 μm. B, close-up of A to show the 0·25–0·5 μm microspheres of which the tunic fibres are composed. Scale bar represents 10 μm. C, section through the inner tunic and overlying mantle muscle in *Mastigophora brevipinnis* (NHM 62231). A number of layers are visible. Scale bar represents 4 μm. D, collapsed intramuscular connective fibres in *Mastigophora* (NHM 31362). The muscle tissue has vanished leaving only the collagenous support structures and scattered 1–2 μm spheres preserved (compare with Text-fig. 2B). Scale bar represents 40 μm. E, close-up of D; some isolated calcium phosphate spheres are visible adhering to the fibres. Scale bar represents 10 μm. F, close-up of surface texture of intramuscular connective fibre from D. The fibre is preserved in clusters of microcrystallites with a framboid-like texture. Scale bar represents 2 μm.



TEXT-FIG. 6. For legend see opposite.

for the mantle and arms retaining their shape when undisturbed. Although no mineral phases were observed in mantle muscle, the structures and bacteria observed resemble those seen in fossil material (compare Text-figs 2B, 4 and 5).

In just two specimens ($n = 19$) of *Alloteuthis* (one each in slow and no diffusion; see Briggs and Kear 1993*a*, 1994) the cells of the upper beak crest area retained some fine structure even after 4 weeks. A fibrous to 'fluffy' texture was evident under the binocular microscope, remaining white even after oven drying. When viewed with the SEM these fibres appear to insert directly onto the beak (Text-fig. 2C). They are 200 μm in length and seem to clump in distinct hexagons of about 70–100 μm diameter. Within these clumps are smaller bundles, about 10 μm in diameter, which could mimic the pattern of beccublast cell imprint on fresh *Alloteuthis* beaks (Dilly and Nixon 1976). Individual fibrils are about 2 μm in diameter and show no evidence of M or Z bands. They probably represent fibrillar phase beccublast cells (= muscle holdfasts; Dilly and Nixon 1976) rather than mandibular muscle itself. Analysis by electron microprobe revealed these fibres to be primarily organic, with no significant mineral phases. Their survival may reflect their structural nature and the protected position of the buccal mass.

Decay of chitinous tissues

In all taxa the beaks survive throughout the duration of the experiments with little alteration (Tables 3–4). SEM analysis shows that the rear edges of the beaks fracture and disintegrate at 10 weeks.

Preliminary analyses with the electron microprobe demonstrate that fresh beaks (*Eledone*, *Todaropsis*) have high levels of sulphur and calcium, and sometimes high silicon and chlorine. Potassium, magnesium and phosphate are present, but not in substantial quantities. Examination of *Alloteuthis* beak material after 4 weeks decay showed that sulphur, calcium and chlorine remain bound within the chitin of the beaks during this period. Other elements in the analysis (Mg, Si, P) decline. Only potassium increases over the 4 week period.

Polygonal imprints of beccublast cells identical to those reported by Dilly and Nixon (1976) are evident on the outer surface of the beaks when the buccal muscle has decayed away (Text-fig. 2D). In untanned areas this pattern becomes distorted or obscured as decay progresses. Similar polygonal imprints occur on the outer surfaces of the suckers (Text-fig. 2E) presumably representing the imprint of 'chitinoblast' cells, the analogues of beccublasts.

In all taxa examined, the radular ribbon is less decay-resistant than the radular teeth which often remain in place until disturbed. The anterior portion of the radula, which carries the old teeth, disintegrates earlier than the posterior portion with its young and newly formed ribbon and teeth.

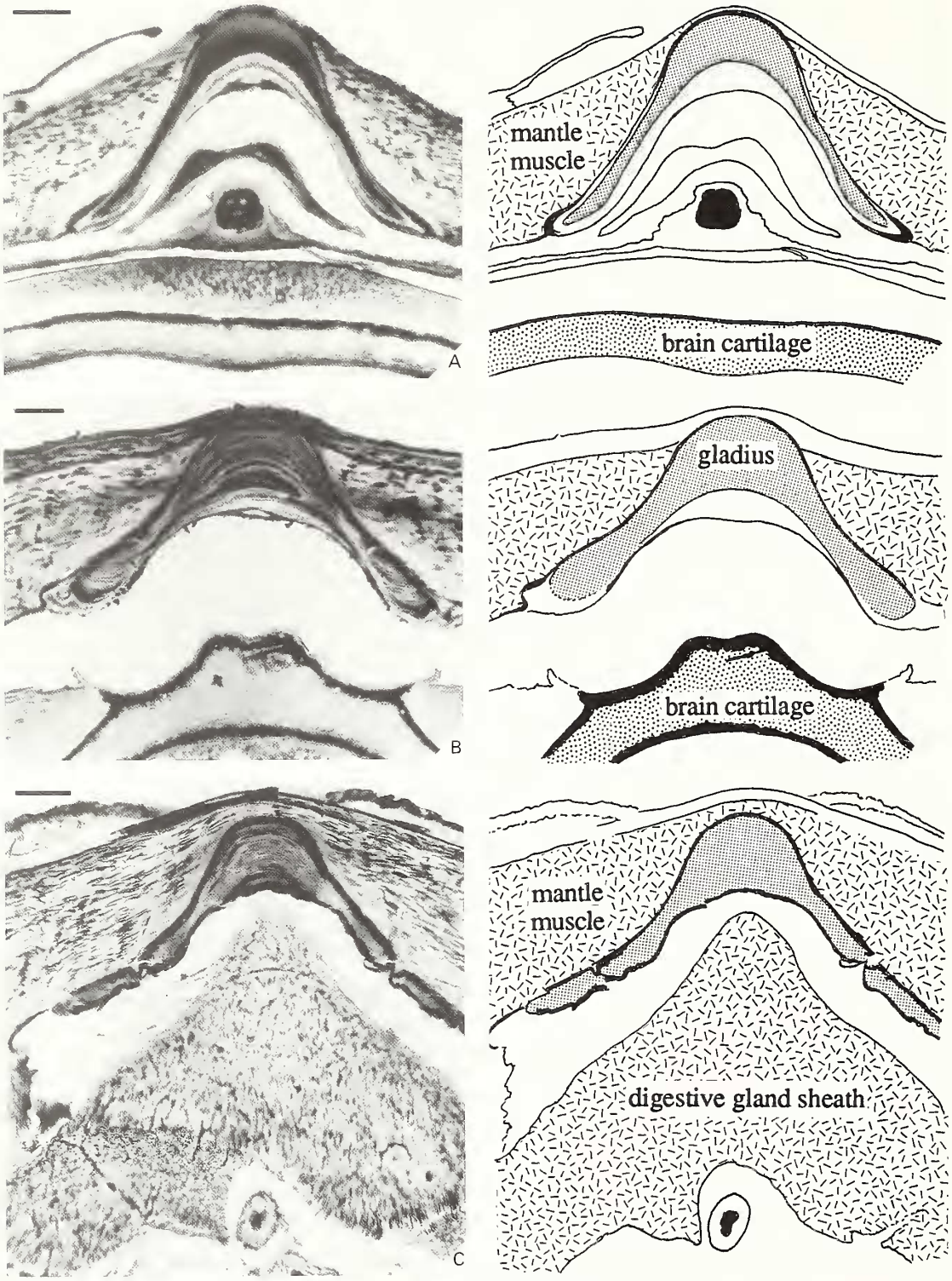
The gladius, despite being untanned, showed little disintegration. No trace was found, however, of the thin chitin of the oesophagus, buccal palps or stomach lining.

Decay of calcareous tissues

Detailed observations of decay were carried out on the statoliths of *Loligo*, as their larger size (1–2 mm) made retrieval and examination feasible (Text-fig. 3A). The statoliths show evidence of surface exfoliation after 1 week under slow diffusion conditions, and there is extensive loss of crystal rhombs in weeks 2–4 (Text-fig. 3B). During decay the statoliths become stained with the pigment released by the carcass, becoming progressively darker.

The statoliths were not recovered beyond week 6. This could be due to their small size which makes them difficult to detect in the disintegrating carcass, their purple-pink colour which makes them impossible to distinguish from the many crystalline fragments which are associated with *Loligo* at this stage, or their complete disintegration or dissolution (vessel pH 7·10–8·46).

TEXT-FIG. 6. A section through the mantle muscle and inner tunic, the underlying gladius, and the muscle forming a sheath around the digestive gland of *Mastigophora brevipinnis*. A, SEM montage of specimen NHM 62231. Scale bar represents 40 μm. B, diagrammatic representation of the section in A. See text for details.



TEXT-FIG. 7. For legend see opposite.

Decay of eye lenses

Initially the eye lenses and surrounding tissues form an intact unit. As early as week 1 the soft tissues have a spongy texture and an imprint is left by forceps tips if they are handled. Soft tissues may remain adhering to the lenses for up to 10 weeks. The eyes remain *in situ* more often in small carcasses (*Alloteuthis*, *Sepiola*) than in the large specimens (*Loligo*), but this is simply because the eyes of the small animals 'rest' on the bottom of the jar and thus have firm support even when the surrounding soft tissue disintegrates. In contrast, *Loligo* eyes are positioned above the substrate at rest, and collapse with decay of the supporting tissues.

The eye lenses themselves cleave along a natural fracture plane (Text-fig. 3C). This can occur as early as week 1 (*Alloteuthis*) or as late as week 50 (*Loligo*). This difference in timing may be a surface area-volume effect. Prior to full cleavage, a fracture is visible running round the lens (day 3 to week 30). Handling of the lenses often causes cleavage along this plane.

FOSSIL COLEOIDS

Musculature

Morphology. Mantle muscle fibres were observed in *Belemnotheutis*, *Mastigophora*, *Geopeltis*, *Loligosepia* and *Plesioteuthis*. Both radial and circular muscle is preserved (Text-fig. 4) but the fibrils or fibres do not always survive. The radial muscles may be represented by raised ridges on the specimens, or they may be missing, leaving a gap between blocks of circular muscle. Where specimens have been conserved by coating in shellac, the varnish fills these gaps and obscures structure. In some specimens (*Belemnotheutis*; BRSMG Ca5242, BRSMG Cd21) the 'muscle' pattern seen is an imprint of the fibres on the surrounding tissues (?tunic).

Longitudinal muscle fibres were observed in *Belemnotheutis* (NHM C.2456), *Mastigophora* (NHM 62231) and *Plesioteuthis* (NHM 83731). In the latter two species these fibres are associated closely with the gladius.

The muscles of the arms or tentacles have preserved fibres only in *Belemnotheutis*, in which they are longitudinal. In one specimen (NHM C.46898) an arm has fractured to reveal longitudinal structure all the way through. The other fibre orientations reported in living coleoids (circular, oblique, helical; Kier 1982, 1988) were not observed.

Ultrastructure. Muscle is preserved in two different forms in material from Christian Malford. The first involves replacement of the muscle by ?sheets of microspheres of 1–2 μm diameter (Text-fig. 4A–E; Allison 1988). The scale of the filaments preserved in this way indicates that they represent muscle fibrils (diameter $1{\cdot}4 \pm 1{\cdot}0$ μm; Ward and Wainright 1972) rather than whole fibres (diameter $5{\cdot}1 \pm 2{\cdot}1$ μm; Ward and Wainright 1972). This form is well represented in *Belemnotheutis*.

The second way in which muscle tissue is preserved is the 'sarcolemma' form, first described in fish from the Cretaceous Santana Formation of Brazil (Martill 1990). The core of the fibres has vanished, leaving only the outer sheath of the sarcolemma intact (Text-fig. 4F). The 'missing' fibrils

TEXT-FIG. 7. Anterior-posterior histological sections (silver staining) through the front portion of a juvenile *Loligo pealei* to show the gladius and associated tissues. Gaps between tissues are histological artefacts. Slides courtesy of Professor J. Z. Young. A, section through the anterior of the gladius at the rear of the head. The upper skin and tunic meet the central keel of the gladius and only a thin layer covers it. Radial and intramuscular fibres are present in the mantle. The layer of chitinoblast cells surrounding the gladius is clear, particularly ventrally. Scale bar represents 100 μm. B, skin and tunic sit directly on top of the keel of the gladius, which rests directly on the brain cartilage. Chitinoblasts surround the gladius, the ventral cells larger than the dorsal, which may be continuous with the inner tunic. Layering within the gladius is evident. Scale bar represents 100 μm. C, section through the body. The gladius is now embedded within the mantle muscle, and associated with the muscular sheath which surrounds the digestive gland. The chitinoblasts are flattened but still visible in places. Scale bar represents 100 μm.

would have had a diameter of 2–7 μm each. Preservation of the sarcolemma, in the absence of fibrils, has only been observed in *Mastigophora*.

Composition. Analysis of both radial and circular muscle fibres in *Mastigophora* shows them to be calcium phosphate. There is no difference in composition between the two muscle forms (Table 5).

Connective tissue. The three main types of connective tissue associated with the mantle musculature in Recent squid (outer tunic, inner tunic and intramuscular fibres) are all preserved in *Belemnotheutis* and *Mastigophora*. The outer tunic is also preserved in *Plesioteuthis* and *Loligosepia*, and possibly in *Geopeltis* (Table 6).

In *Belemnotheutis* the tunic still preserves the parallel rows of fibres in alternating sheets (Text-fig. 5A, C) which are bisected by the sagittal axis of the specimen at 15–16° (an angle of $27 \pm 1{\cdot}0°$ is recorded in living *Loligo* and *Lolliguncula*; Ward and Wainright 1972). The fibres in the tunics are preserved as microspheres, 0·25–0·5 μm in diameter (Text-fig. 5B).

The number of sheets in the tunics varies, but at least three are present in *Belemnotheutis*. In *Mastigophora* (NHM 62231) there are four to five in the inner tunic, two to three in a tunic-like layer dorsal to the gladius, and one or two in a similar layer ventral to the gladius (layers ii, iv and vii respectively; Text-fig. 6).

The intramuscular connective tissue fibres are best preserved in *Mastigophora* (Text-fig. 5D–F). These fibres are 5–10 μm in diameter and are fragmented into sections 20–150 μm long. The texture of these fibres is reminiscent of framboids, in that they consist of spheres composed of crystallites of $< 0{\cdot}1$ μm (Text-fig. 5F). Ward and Wainright (1972) measured intramuscular connective tissue fibres of diameter $2{\cdot}6 \pm 0{\cdot}74$ μm in living material.

A section through Mastigophora *from Christian Malford*

In specimen NHM 62231 a section through the gladius and surrounding tissues revealed nine separate layers (Text-fig. 6). These are:

(i) a muscle layer, about 70 μm thick, composed of microspheres of 1–2 μm diameter, texturally similar to the muscle preserved in other specimens, but with a lower order of information retained;

(ii) a layer about 10 μm in total thickness, consisting of four to five sheets, representing the inner boundary tunic associated with the muscle layer (i) (Text-fig. 5C);

(iii) another microspherulitic layer running parallel to the gladius, with a total thickness of about 60 μm, with bands of smoother material within it;

(iv) a thin (*c*. 2–3 μm) layer of compacted microcrystallites or spheres similar to those evident in *Belemnotheutis* tunic (Text-fig. 5A–B);

(v) a massive layer, thickness *c*. 40 μm, with a fracture reminiscent of the desiccation cracks in dried beak material;

(vi) a layer about 80 μm thick, with a conchoidal fracture and banded structure. Some of the fractures from layer (v) run parallel to or into this, so it may be a different face of the same material. The bands look like growth lines, with finer lines visible within broad striation. Broad bands are about 1–2 μm and find bands about 0·3 μm thick. Layers (v) and (vi) represent the gladius.

(vii) another layer, *c*. 3 μm thick, of tunic-style microspheres 0·25 to 0·5 μm in diameter;

(viii) disorganized microspheres of 1–2 μm diameter representing muscle tissue with low order preservation that grades into layer (ix);

(ix) sarcolemma style preservation. The sarcolemma sheaths appear to have a granular texture, composed of crystallites/grains about 0·1 μm in size (Text-fig. 4F). 'Muscle'-sized microspheres are scattered around, but not organized into fibres. The hollows in the sarcolemma (= site of fibres) run parallel to the gladius. The combined thickness of layers (viii) and (ix) is about 200 μm.

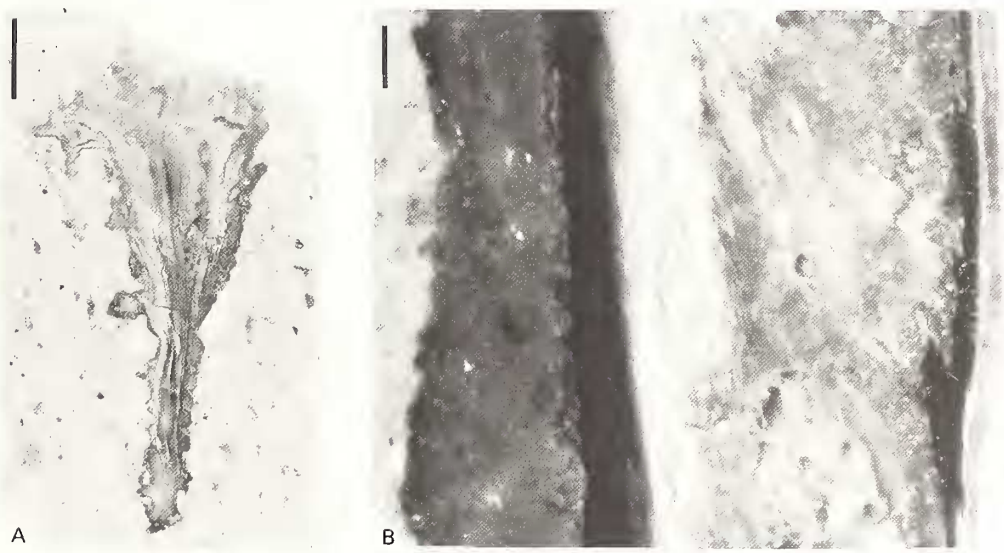
Comparing the structures with living material (see Text-fig. 7), the *Mastigophora* specimen is interpreted as a section from the dorsal mantle to the muscular sheath of the digestive gland. Layers (i), (viii) and (ix) are undoubtedly muscle, the last two representing the digestive gland sheath which sits ventral to the gladius (Text-fig. 7C). The banded structure in layer (ii) is the inner tunic of the mantle muscle.

Layer (iii) does not retain enough structure for a precise interpretation. It may represent either a second muscle band, or epithelial tissue associated with the secretion of the gladius. The mantle muscle is not split into two layers in modern coleoids, so the latter interpretation is more likely. Examination of recent material shows the presence of a layer of epithelial cells surrounding the gladius (Text-fig. 7). Under the light microscope these are similar in morphology to the odontoblasts associated with the radular sac (Nixon 1968), the beccublasts reported by Dilly and Nixon (1976) and the 'chitinoblasts' of Kear (1990). Because of their association with the gladius, layers (iv) and (vi) are suggested to be the remains of these chitinoblast cells. Layers (iii) and (iv), in combination, may be the dorsal chitinoblasts: (iii), responsible for chitin secretion; and (iv), the remains of the fibrillar material which anchors the mantle muscle to the pen.

Complex layering of this type is also preserved in *Belemnothentis antiquus*. In the tissues dorsal to the gladius of specimen NHM C.2456 twelve layers can be distinguished using the binocular microscope. The topmost two are identifiable as tunic layers (see Text-fig. 5A), and the third as muscle fibres (Text-fig. 4A–D). Layer (viii) shows very fine fibres running at 60° to the orientation of the muscle fibres and may be another tunic type layer. No structure was evident in the other layers.

A section through Geopeltis *from Charmouth*

An incomplete specimen (BRSUG 25602) of the loligosepiid *Geopeltis*, preserved in a nodule from the Lower Lias of Black Ven, Charmouth, Dorset, was studied. The form of the gladius identifies the specimen, which preserves the ink sac near the midline.



TEXT-FIG. 8. Polished sections through the gladius and associated soft tissues of *Geopeltis* sp. from Charmouth, Dorset (BRSUG 25602). A, the edge of the rachis of the gladius, with layered structure clearly visible. Sparry calcite is present in the wider portion to the top of the photograph. Scale bar represents 500 μm. B, counterpart of the specimen. The thin layers of the gladius are to the right, with fibrous material overgrown by calcite immediately beneath. The other bands reveal no ultrastructure. Scale bar represents 100 μm.

The broad gladius is about 1 mm in total thickness. A layered structure is evident, with alternating brown and yellow-white bands. At the very edge of the gladius there are eight layers present (Text-fig. 8; compare with the cross sections of modern gladius material in Text-fig. 7). On the counterpart four layers were visible with the binocular microscope, and a further two revealed by the electron microprobe. Fibrous structure is visible within the surface layer (Text-fig. 8B); individual fibres have clearly defined edges with smaller fibrils running obliquely within them. This may represent the original structure of the gladius.

Soft tissues are represented by white to brown material. On the part this 'organic' material appears to be slumped on and around the gladius, with no ultrastructure preserved. Sparry calcite is associated with this material. There appear to be two generations of diagenetic calcite present. On the counterpart there is fibrous structure within the 'organic' material (Text-fig. 8B) and it is layered, different layers showing different degrees of ultrastructural preservation and overgrowth by calcite.

Similar layered structure is preserved in the gladius and muscle tissue of coleoids (*Trachyteuthis hastiformis*, *Plesioteuthis prisca*) from the Solnhofen limestone (NHM 83730 and 83731). Six layers are evident in a section of *Trachyteuthis* under the binocular microscope: five of these are gladius and the sixth possibly mantle muscle. Striations, fibres and sub-layers are evident within the main bands of gladius material. This structure may reflect original morphology. In *Plesioteuthis* six gladius and two possible mantle muscle layers are visible.

Composition of fossil material

Analysis of muscle tissues from *Mastigophora* (Table 5) shows no difference in the composition of radial and circular muscle.

Calcium phosphate and calcium carbonate (Table 5) were present in material from the gladius and ink sac of *Geopeltis*. In the gladius the proportions vary from almost pure fluorapatite (layers 2, 4 and 6), through a phosphate–carbonate mixture (layers 3 and 5), to high carbonate (layer 1). Material from the ink sac is also calcium phosphate (fluorapatite) with some carbonate, and a low organic content (Table 5). These compounds reflect diagenetic mineralization and not original gladius or ink composition. Beyermann and Hasenmaier (1973) demonstrated the presence of melanin in the preserved ink sacs of specimens of *Geoteuthis* from the Posidonienschiefer (Lias) of Germany using infrared spectrometry. The calcium carbonate in the gladius may be the diagenetic sparry calcite abundant elsewhere in the specimen.

Hewitt and Wignall (1988) analysed a specimen of *Trachyteuthis* from the Kimmeridge Clay (Late Jurassic) of England and determined that it was composed of francolite. They interpreted this as implying an originally phosphatic composition, i.e. as a diagenetic replacement of a shell composed of chitin and brushite. Hirschler *et al.* (1990) demonstrated experimentally that aragonite can be replaced by calcium phosphate. Analyses of fossil material (above) and experimental results (Briggs and Kear 1994) confirm that a range of original tissue compositions may be altered to calcium phosphate. Thus the 'shell' of *Trachyteuthis* may have been originally aragonitic in composition.

DISCUSSION

The precipitation of crystals

A striking result of the decay experiments was the precipitation of crystals of magnesium phosphate, particularly in association with *Loligo*. Experiments run under the same conditions of slow diffusion on the crustaceans *Crangon* and *Palaemon* (Briggs and Kear 1994) commonly resulted in the formation of crystal bundles of aragonite. However, laths of magnesium phosphate formed on a *Palaemon* carcass that had decayed under these conditions for 75 weeks. The replication of soft tissue in calcium phosphate was much more prevalent in experiments run under different 'closed' conditions (Briggs and Kear 1994). Whether such soft tissue mineralization can be induced in similar experiments on coleoid cephalopods remains to be investigated.

TABLE 7. Habitat, post-mortem effects and preservation potential of living coleoid families. Data from Schäfer (1972), Clarke *et al.* (1979), Clarke (1985), Nesis (1987), Lipinski and Jackson (1989), Croxall and Prince (1994), Jackson and Mladenov (1994) and this study. * Positive post-mortem buoyancy is assumed where the coleoid is ammoniacal, although data for all families are not available. Classification after Clarke (1988).

			Buoyancy		
		Habitat	Type	Life	Post-mortem*
Sepiida					
Spirulidae	Oceanic	Midwater	Shell	Neutral	
Sepiidae	Shelf	Benthic	Shell	Neutral	Positive
Sepiadariidae	Shelf	Benthic	Shell	Neutral	
Sepiolida					
Sepiolidae	Shelf	Benthic	Muscular	Negative	Negative
Idiosepiidae	Shelf	Benthic	Muscular	Negative	
Teuthida					
Pickfordiateuthidae	Oceanic	Midwater	Muscular	Negative	
Loliginidae	Shelf	Midwater-benthic	Muscular	Negative	Negative
Lycoteuthidae	Shelf-oceanic	Midwater	Ammonia	Neutral	Positive
Enoploteuthidae	Oceanic	Midwater	Ammonia	Negative	
Ancistrocheridae	Oceanic	Midwater-benthic	Ammonia	Neutral	
Pyroteuthidae	Oceanic	Midwater	?	Negative	
Octopoteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Onychoteuthidae	Oceanic	Midwater-benthic	Ammonia	Neutral	Positive
Cycloteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Gonatidae	Oceanic	Midwater-benthic	Oil	Neutral	?Positive
Psychroteuthidae	Oceanic	Midwater	?	?Negative	?Negative
Lepidoteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Pholidoteuthidae	Oceanic	Midwater	?	Negative	
Architeuthidae	Oceanic	Midwater-benthic	Ammonia	Neutral	Positive
Histioteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Neoteuthidae	Oceanic	Midwater	?	Negative	Positive
Bathyteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Ctenopterygidae	Oceanic	Midwater	?	Negative	
Brachioteuthidae	Oceanic	Midwater	?	Negative	
Batoteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Ommastrephidae	Shelf and slope	Midwater-benthic	Muscular	Negative	Both positive and negative records
Thysanoteuthidae	Oceanic	Midwater	Muscular	Negative	
Chiroteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Mastigoteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Promachoteuthidae	Oceanic	Midwater	?	?Negative	
Grimalditeuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Joubiniteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Cranchidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Vampyromorpha					
Vampyroteuthidae	Oceanic	Midwater	Sulphate	Neutral	
Octopoda					
Cirroteuthidae	Oceanic	Benthic	Sulphate	Neutral	
Stauroteuthidae	Oceanic	Benthic	Sulphate	Neutral	
Opistoteuthidae	Oceanic	Benthic	Sulphate	Neutral	
Bolitaenidae	Oceanic	Midwater	Sulphate	Neutral	
Amphitretidae	Oceanic	Midwater	?	?	
Idioctopodidae	Oceanic	Benthic	?	?	
Vitreledonellidae	Oceanic	Midwater	Sulphate	Neutral	
Octopodidae	Shelf	Benthic	Muscular	Negative	Negative
Tremoctopodidae	Oceanic	Midwater	Muscular	Negative	
Ocythoidae	Oceanic	Midwater	Muscular	Negative	
Argonautidae	Oceanic	Midwater	Muscular	Negative	
Alloposidae	Oceanic	Midwater	Sulphate	Neutral	

Differential survival of chitinous structures

The thick, tanned α chitin of the beaks survived longest and with least damage in the experiments (for 50 weeks in *Loligo*). Buccal masses are routinely allowed to rot for a few days in a jar of sea or tap water to extract beaks for taxonomic purposes because this avoids damaging untanned areas (Clarke 1986; Kear 1990). The tanned portions of the radula (also α chitin; see Table 2) persisted longer than the untanned: the teeth may survive even when the ribbon has disintegrated. The pen (untanned β chitin) also suffered little damage, but the oesophageal cuticle (untanned α) and the stomach lining (untanned γ) do not seem to survive. The suckers (β chitin, untanned) also degenerated quickly but they are preserved in one specimen of *Belemnotheutis* (BRSMG Ca5240) from Christian Malford (Donovan and Crane 1992). Thus thicker, tanned chitinous structures have a higher preservation potential.

Cephalopod beaks are robust as evidenced by their survival in the digestive tract of marine vertebrates (whales, seals, albatrosses). Sperm whales find them indigestible and regurgitate large quantities of beaks, which can be found covering the seafloor at certain localities (Clarke 1962). Aggregations of beaks have not been reported from the fossil record, even though the earliest record of sperm whales (Physeteridae) is lower Miocene (Stucky and McKenna 1993), and earlier marine vertebrates preyed on cephalopods (see e.g. Pollard 1968; Martill 1986). Isolated fossil examples, however, are known (e.g. Dzik 1986).

Other decay resistant structures

Traces of the brain cartilage (collagen) may last up to 20 weeks. As other collagenous tissues (tunics, sarcolemma) preserve well, the brain cartilage would also be expected to survive in fossil material. Fischer and Riou (1982*a*) interpreted paired structures behind the eyes in *Romaniteuthis gevreyi* (Callovian of La Voulte-sur-Rhône) as brain cartilage. In other material, extensive preparation in the head region may be required to reveal the presence of the cartilage.

The statoliths (aragonite) exfoliate during decay and eventually vanish. This disappearance may be real or an artefact of sampling technique. Isolated statoliths are found in the fossil record (Clarke and Fitch 1975; Clarke and Maddock 1988), but none has been reported associated with a body fossil. Possible explanations include: (1) isolated statoliths may have passed through the gut of a predator before reaching the seafloor; (2) exceptionally preserved fossils would need sectioning or extensive preparation to reveal the presence of statoliths within the head; and (3) the statoliths may have recrystallized during diagenesis.

During decay the eye lenses eventually cleave and stain, but seem otherwise undamaged. They are preserved in coleoids from La Voulte-sur-Rhône (Fischer and Riou 1982*a*, 1982*b*) but have not been reported from Christian Malford. Eye lenses follow the same pattern of cleavage and are stained orange-brown when they undergo digestion by vertebrates (dogfish and albatross). In addition, digested eyes exfoliate, the various layers of the lens starting to peel away from the centre. This may represent a terminal stage of disintegration not reached during the course of our decay experiments.

The influence of buoyancy on preservation potential

In life, coleoids can be divided into two groups (Table 7): negatively buoyant (14 families; Clarke 1985) and neutrally buoyant (25 families; Clarke 1985). The muscular, active swimmers (Loliginidae, Ommastrephidae) which are the target for commercial squid fisheries are typical examples of negatively buoyant species. Living coleoids achieve neutral buoyancy by four different methods (Clarke *et al.* 1979; Clarke 1985). These are: (a) the use of gas-filled shells in 'true' cuttlefishes and Spirulidae; (b) substitution of sulphate ions by chloride ions within the body tissues of some oceanic octopods, e.g. Cirroteuthidae, and the Vampyroteuthidae; (c) storage of low density fats in the digestive gland in the Gonatidae; and (d) the accumulation of ammonium chloride ions in sixteen families of oceanic squid, e.g. Architeuthidae, Cranchiidae (Table 7).

A freshly dead or dying coleoid may either sink or float. Observations from aquarium animals, decay experiments (Schäfer 1972; Lipinski and Jackson 1989), and the mass mortalities associated with spawning (*Illex illecebrosus* in Newfoundland, *Loligo opalescens* in California, and *Loligo vulgaris reynaudii* in South Africa) indicate that the majority of negatively buoyant animals remain so at death. Ommastrephids, however, have been observed floating after mass mortalities and stranded on beaches. These events represent death during the migration phase of the life cycle, not post-spawning mortality (M. R. Clarke, pers. comm.).

The normally neutrally buoyant *Sepia*, with its large internal shell, floats in the early stages of decay (Schäfer 1972; Lipinski and Jackson 1989; personal observations), indicating a rapid post-mortem shift to positive buoyancy. This may take place before the animal is dead; morbid animals lose their ability to regulate buoyancy. Subsequent loss of the 'cuttlebone' as *Sepia* decays allows the rest of the carcass to sink (Lipinski and Jackson 1989). Conversely, our experimental observations on *Loligo* heads indicate that negatively buoyant species may be buoyed up by decay gasses after a period on the sea floor (depending on the depth of water: see Allison *et al.* 1991).

Kondakovia longimana is an ammoniacal squid (family Onychoteuthidae). Analysis of its tissues show that it contains almost double the ammonia found in other species which use this buoyancy mechanism (329·4 mM compared with 199·6–206·9 mM in *Moroteuthis* of the same family) and that it has very loosely arranged bundles of muscle fibres, with the ammoniacal fluid filling the 'gaps' (Lu and Williams 1994). This tissue chemistry results in post-mortem positive buoyancy. Most records of *Kondakovia* are from predator stomachs (albatrosses, petrels, whales) and sightings of dead individuals at the sea surface. There are very few records of live captures (Lu and Williams 1994). As albatrosses are incapable of diving to great depths (6–12 m; Croxall and Prince 1994) they are assumed to be scavenging on *Kondakovia* floating at or near the surface (Lu and Williams 1994).

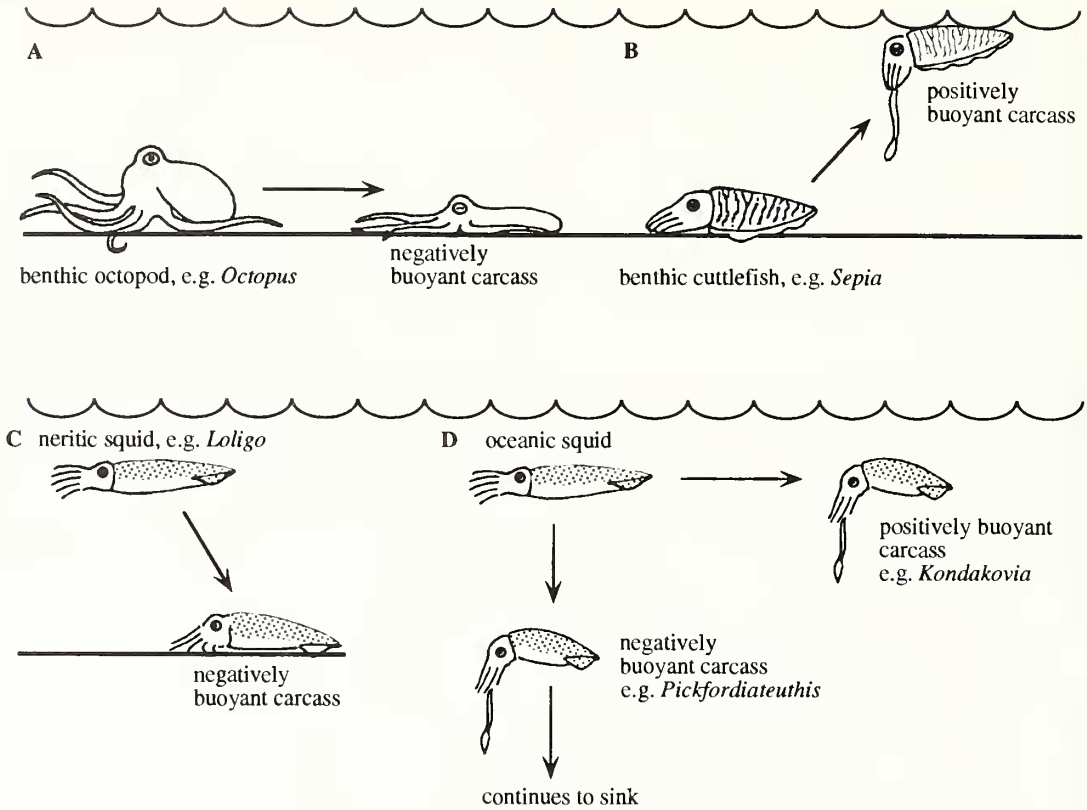
The giant squid *Architeuthis* is occasionally found stranded or floating at the sea surface. Whilst some of these specimens are undoubtedly the regurgitations of sperm whales, several have been reported as still alive (Verrill 1880), showing that the ammoniacal *Architeuthis* was positively buoyant when dying.

In animals that are neutrally buoyant at death and settle rapidly to the sea-floor the tentacles remain concealed within the cone of the arms. By contrast, in morbid and dying *Sepia*, or in carcasses that are handled, the tentacles slip out and hang loose in the water (Text-fig. 9). Hence, an exceptionally preserved animal which only displays four pairs of arms may have the tentacles concealed. Thus *Plesioteuthis* presumably had tentacles even though they have not been recorded.

A morbid animal which floats will be spotted by scavengers (including cannibalistic conspecifics) very easily, and is also unlikely to get buried. In 'sinking' species an annual event such as a spawning mass mortality will attract scavengers in large numbers so carcasses are unlikely to be left undisturbed. Carcasses of *Loligo opalescens* are rapidly removed from the shelf spawning grounds into deeper water by currents (R. Starr, pers. comm.). A similar process may explain the mass accumulations of belemnite rostra in some localities (Doyle and MacDonald 1993).

Species with the highest potential for fossilization are those benthic shelf species that remain negatively buoyant after death (*Octopus*, *Sepiola*) or those which spawn in mid-water producing a neutrally buoyant egg mass and a negatively buoyant carcass (e.g. the Ommastrephidae) which may fall into anoxic bottom water. Table 7 categorizes the ecology of modern cephalopods and their post-mortem buoyancy.

Belemnotheutis possessed a phragmocone and might be expected to mimic *Sepia* physiologically and be neutrally buoyant in life and positively buoyant after death. However, the occurrence of exceptionally preserved material seems to indicate that there was little or no positive phase, the carcass reaching the seafloor rapidly after death.The phragmocone may not have represented as large a proportion of the body in *Belemnotheutis* as it does in *Sepia*, so it may not have been capable of refloating the carcass. If the high proportion of living teuthids that become positively buoyant after death (Table 7) is paralleled in extinct genera, it requires an agent such as rapid burial and/or a soupy substrate (Martill 1993) to be invoked where the soft tissues of the fossil forms are preserved (Allison 1988).



TEXT-FIG. 9. Cephalopod habitats and buoyancy (before and after death). A, benthic octopods remain negatively buoyant after death and have a relatively high preservation potential. B, cuttlefish have positive post-mortem buoyancy and a low preservation potential. C, neritic squid have negative post-mortem buoyancy and a high preservation potential. Tentacles do not extend at death. D, oceanic squid families may have either positive or negative post-mortem buoyancy. In negatively buoyant families preservation potential is lower than for their neritic counterparts, and decay will commence before reaching the seafloor. The potential for fossilization is lower still in positively buoyant species. In both cases tentacles will extend during movement of the carcass through the water column.

The influence of sex and maturity on preservation potential

In our experiments the ovary maintained the three dimensional shape of the rear portion of the body, and may be responsible for holding the disintegrating mantle in place. Whilst spermatophores and sperm may survive some time (10 days in *Sepiola*) they do not show the same cohesion. However, as it is energetically more expensive to produce eggs than sperm, females divert more of their resources to reproduction than males (an extreme case being the disintegration of the mantle in *Moroteuthis ingens*; Jackson and Mladenov 1994). In spent animals, therefore, males are more likely to be preserved than females. A further complication is that eggs, in common with other tissues, swell through osmosis as they decay. In a mature *Sepiola* carrying large eggs, this process tears the body apart. In *Alloteuthis*, of mid range maturity, the presence of an ovary enhanced the preservation of the body outline (see above). In an immature female (ovary undeveloped) or male, presumably a 'normal' disintegration pattern would be seen.

As determination of sexual maturity or gender in fossil coleoids is problematic (although sexual dimorphs can be recognized, e.g. Doyle 1985), such biases may be difficult to identify.

Phylogenetic implications of ultrastructural preservation

The discovery of a 'modern' mantle structure in Jurassic cephalopods which possessed a phragmocone (*Belemnotheutis*) and in those without (*Geopeltis*, *Loligosepia*, *Mastigophora*, *Plesioteuthis*) is of phylogenetic interest. It supports the view (Donovan 1977; Doyle *et al.* 1994) that the squid grade of organization had already evolved by the Jurassic. Other Jurassic and Cretaceous genera appear to have mantle tissue with a similar structure to that reported here, although they have not been examined using the SEM. They include *Sueviteuthis* (Toarcian), *Teudopsis* (Toarcian), *Kelaeno* (Tithonian), *Leptotheuthis* (Tithonian), *Paraplesioteuthis* (Tithonian), *Trachyteuthis* (Tithonian) and *Dorateuthis*? (Santonian). The Phragmoteuthidae have been regarded as the stem group ancestral to these genera (Donovan 1977). A Toarcian Phragmoteuthid from Holzmaden, Bavaria, (in the Museo Civico di Storia Naturale, Milan) shows what appear to be packets of radial muscle, up to 3 mm long, under the optical microscope, in contrast with the longer bands in other fossil coleoids and in Recent squids. This is tentatively regarded as a more primitive condition.

Squid mantle (Ward and Wainwright 1972) differs from octopus mantle (Gosline and DeMont 1985) in its detailed structure. The system of collagen tunics and intramuscular fibres in squids prevents longitudinal extension of the mantle during contraction of the circular muscles (Wells 1988). In octopods the same function is performed by longitudinal muscles, which are absent from the main part of the squid mantle. The octopod arrangement may permit greater flexibility of the mantle, at the expense of higher energy expenditure (Gosline and DeMont 1985).

The possession of tunics and intramuscular collagen fibres links *Belemnotheutis* and *Mastigophora* to living Decabrachia (Teuthida, Sepiida and Sepiolida) rather than Octobrachia (Cirroctopoda and Octopoda). *Belemnotheutis* and the related *Acanthoteuthis* (Donovan and Crane 1992), both with phragmocone and ten undifferentiated arms, must stand close to the ten-armed forms from which the arm arrangements in living Octobrachia and Decabrachia were derived (Bandel and Boletzky 1988; Boletzky 1992). However, they had already evolved the decabrachia type of mantle. *Mastigophora* (number of arms unknown, without phragmocone) represents a further stage toward modern squids, whether or not it lay on or near the direct line of evolutionary descent.

The presence of squid-type musculature in *Belemnotheutis* calls into question the current systematic placing of the genus in Belemnitida (Jeletzky 1966; Bandel and Kulicki 1988) accepted by Donovan and Crane (1992). The Belemnoidea (Aulacocerida, Belemnitida and Diplobelida) are now considered to have diverged from the ancestors of Phragmoteuthida and modern squids in the Late Palaeozoic (Doyle *et al.* 1994). The structure of the mantle musculature in typical Belemnoidea (i.e. with well-developed rostrum) is unknown. If *Belemnotheutis* is a belemnitid then the squid-type mantle structure had either evolved by the Late Palaeozoic, or evolved independently in Belemnitida and in Loligosepiida (which include Mastigophoridae) subsequently. Both these possibilities are unlikely, and the position of *Belemnotheutis* remains to be resolved.

If the highly specialized mantle structure of squids evolved only once, as seems likely, then the monophyletic group of Recent squids and cuttlefish (Clarke 1988) can be extended back in time to include the fossil forms discussed in this paper. The mantle structure of the Octobrachia may have evolved from that of the squids or, more probably, they represent a separate monophyletic group.

The presence of typical squid mantle structure in the Jurassic suggests that coleoid physiology had evolved by that time. Wells *et al.* (1992) contrasted the physiology of coleoids with that of *Nautilus*, which can survive in conditions of very low oxygen tension, whereas coleoids with their more active life style and high metabolic rate cannot. The fossil record of coleoids, apart from the Aulacocerida, before the Jurassic is almost non-existent, but coleoid organization probably began to evolve in Phragmoteuthida at least as early as the Late Permian, and had given rise to typical squids by the Late Norian (Triassic; Reitner 1978).

CONCLUSIONS

Although the three coleoid species investigated, the squids *Alloteuthis subulata* and *Loligo forbesi*, and the sepiolid *Sepiola atlantica*, degraded in a similar series of stages and at comparable rates under experimental conditions (Tables 3, 4) a range of factors, including habitat and buoyancy (Table 7), will ensure a diversity of preservation potential among coleoids.

The amount of phosphate required for the extensive mineralization of specimens from Christian Malford and other localities must have exceeded that available in the carcass itself. The additional source was presumably phosphate concentrations that built up in the sediment beforehand (Allison 1988; Martill 1988). Some decay is necessary to promote mineralization, and all the fossil specimens show evidence of degradation. The experiments on modern squid show that ultrastructural detail in muscle may be lost in as little as 1·5 days (under conditions of 'slow diffusion': Briggs and Kear 1993*a*, 1994) although not all the muscle tissue decays at the same time. Experiments on mineralization indicate that the formation of calcium phosphate is more prevalent under 'closed' conditions where it takes some time to initiate after the onset of decay (two weeks in shrimp experiments: Briggs and Kear 1993*b*, 1994). Precipitation then builds up over a period of weeks.

Detailed documentation of the ultrastructural detail preserved in phosphatized soft tissue (as opposed to the texture of mineralization) has previously been confined to taxa from the Lower Cretaceous Santana Formation of Chapada do Araripe, Brazil (Martill 1988, 1989, 1990; Wilby and Martill 1992) and the Upper Jurassic Cordillera de Domeyko of Chile (Schultze 1989). Coleoid cephalopods have not been reported from the Santana Formation and there are no SEM studies of the rare examples from the Cordillera de Domeyko (Schultze 1989). This investigation therefore demonstrates, for the first time, the range of tissues that may be preserved with ultrastructural detail in phosphatized fossil coleoids. This study emphasizes that this kind of preservation is not confined to a small number of Konservat-Lagerstätten, but is more widespread (see, for example, Briggs *et al.* 1993). It is becoming increasingly clear that there is considerable potential for informative histological studies of the soft tissues of a range of fossil organisms.

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APPENDIX: SPECIMENS EXAMINED FOR THIS STUDY

NHM, Natural History Museum; BRSMG, Bristol City Museum; BRSUG, University of Bristol, Geology Department; *, material removed for examination by scanning electron microscopy; †, material removed for examination by electron microprobe.

Species	Repository	Specimen number	Locality
Belemnotheutis antiquus	NHM	C2456*, C46898*	Christian Malford, Oxfordshire
	BRSMG	Ca 5240 (Lectotype)	Christian Malford, Oxfordshire
	BRSMG	Ca 5242 (Type specimen)	Christian Malford, Oxfordshire
	BRSMG	Cb 7661, Cd 18a, b, Cd 21, Cd 22a, Cd 22b	Christian Malford, Oxfordshire
Geopeltis simplex	NHM	C580	Boll, Wurtemberg, Germany
Geopeltis sp.	BRSUG	25602†	Black Ven, Charmouth, Dorset
Loligosepia (= *Geoteuthis*)	NHM	C5260	Dumbleton, Gloucestershire
	NHM	C9922	Gloucestershire
	NHM	C12619	Near Ilminster, Somerset
Mastigophora brevipinnis	NHM	31362*†, 46964*, 62231*	Christian Malford, Oxfordshire
	BRSMG	Cd 32, Cd 37, Cd 38a, b, Ce 17967a, b	Christian Malford, Oxfordshire
Plesioteuthis prisca	NHM	83731, 83732, C1046, C46284a, C46847, C46869, C46880, C46886	Solnhofen, Germany
Trachyteuthis hastiformis	NHM	83730	Solnhofen, Germany